

**BIONOMICS OF *EVYLAEUS COMAGENENSIS*
(KNERER AND ATWOOD) (HALICTIDAE), A FACULTATIVELY
POLYGYNOUS, UNIVOLTINE, BOREAL HALICTINE BEE**

S. W. T. BATRA

Beneficial Insects Laboratory, Bldg. 476, United States Department of Agriculture,
Beltsville, Maryland 20705.

Abstract. — *Evylaeus comagenensis* (Knerer and Atwood) (Hymenoptera: Halictidae) is a boreal carinate species with solitary to nearly unique semisocial or quasisocial behavior. In the Adirondacks of northern New York, it was at the southern limit of its range, which may be restricted by the deleterious effects of summer heat and drought on its brood. The brood was in exceptionally shallow subterranean clusters (combs) of delicate earthen cells. Its nest architecture, phenology, associates, and sociobiology are discussed.

Key Words: nesting, quasisocial, semisocial, polylectic

There are about 2000 species of halictine bees worldwide (Sakagami et al. 1982). They include many solitary species, as well as species that share nests in a variety of social arrangements (Michener 1974). The genus *Evylaeus* consists of small, black, inconspicuous bees that are closely related to *Lasioglossum*, and are included in this genus by some taxonomists. *Evylaeus*, a primarily Palearctic genus, includes 81 species in the Western Hemisphere (Moure and Hurd 1987). Most research concerning the biology of *Evylaeus* has been performed in Europe and Japan; only five North American species have been investigated (Moure and Hurd 1987, Packer et al. 1990a, b).

Evylaeus comagenensis (Knerer and Atwood) belongs to the 'carinate' group, in which the females have a carina on the posterior edge of the propodeum (Svensson et al. 1977), and it is closely related to *E. niger* (Viereck). Bees in this group often construct their subterranean cells so that they form delicate earthen combs, surrounded by air-filled cavities. Several *Evylaeus* species be-

gin nesting each spring, when groups of overwintered females cooperatively construct each nest. This polygynous condition may be quasisocial if all females perform all duties, including oviposition; or it may be semisocial if there is a division of labor, with some females laying eggs and others performing other duties. In species of *Evylaeus* that may facultatively begin nests in spring polygynously, the colonies continue to produce broods in the summer in an eusocial manner. Thus the nest-founding females (foundresses) become egglayers (queens), while their daughters stay in their natal nests as workers, e.g. *E. nigripes* (Lep.) (Knerer and Plateaux-Quénu 1970) and *E. linearis* (Schenck) (Knerer 1983). *Evylaeus comagenensis* is unusual because it is univoltine, and thus does not have any eusocial phase. The only other univoltine, polygynous species is *Dialictus problematicus* (Blüthgen) from northern Japan (Sakagami et al. 1984). Strictly polygynous (quasisocial or semisocial) colonies of Hymenoptera are rare, and, therefore, *E. comagenensis* is of

unusual interest for comparative investigations of the probable evolution of insect societies.

HABITAT

I discovered nests of *E. comagenensis* in 1986 during an investigation of *Andrena* (*Scapteropsis*) *alleghaniensis* Viereck, which shared the nesting site (Batra 1990). Nests were aggregated in an insolated south-easterly facing road cut in the Adirondack Mountains of northern New York (44°12'N; 73°55'W), at an elevation of 668 m (2035'). This may be the southernmost extension of the range of this boreal bee, which occurs from north of the Arctic circle at Inuvik, N.W.T. (Sakagami and Toda 1986) to Ontario. According to Knerer and Atwood (1964), it is not found south of 45°N, but Svensson et al. (1977, Fig. 23) illustrate a record from the Appalachian Mountains in Pennsylvania. Packer (pers. comm.) found *E. comagenensis* to be rare in southern Ontario but very common to the north.

The soil in which the bees nested consisted of well-drained glacial outwash, a mixture of fine, loose, dustlike sand, pebbles, and cobbles, without surface vegetation. The surrounding area was covered with mature mixed northern hardwood and softwood forest. At the time that *E. comagenensis* was active, species of *Acer*, *Prunus*, *Amelanchier*, and *Viburnum*, as well as forest-floor herbs, were blooming. According to Knerer and Atwood (1964), this species is polylectic. I found pollen of many species in the provisions and in the digestive tracts of adults, which confirms their report.

I carefully excavated nests in May and June, 1987 and 1989. Nest contents were preserved, reared, dissected, and evaluated, and foragers were collected to determine each bee's social rank. I could not visit the site during the exceptionally hot, dry spring of 1988.

NEST ARCHITECTURE, PHENOLOGY, AND ASSOCIATES

Each of the 21 complete nests that I examined contained a single brood-cell comb (Fig. 1). Most lacked tumuli and were closed at their entrances. Open nest entrances were irregular, cryptic, unguarded, and about 2.5 mm in diameter. The cluster of brood cells was very shallow, the topmost cells being 1.5–5.0 (\bar{x} = 3.32) cm below the surface of the eroding sand. The lowest cells were 4.5–7.5 (\bar{x} = 6.0) cm deep. Clusters (brood combs) were 1.5–4.0 (\bar{x} = 2.6) cm high and 1.5–3.5 (\bar{x} = 2.0) cm wide, and were without lateroids. They were supported in the 4–7 mm-wide cavities by several earthen pillars. Nests contained 1–12 (\bar{x} = 5.5) cells. One nest that had only a single cell lacked a cavity, and a nest with two cells had an incipient cavity, indicating that the initial cells were made before the surrounding cavity was excavated. Nests that contained only one female had 1–7 (\bar{x} = 3.6) cells and polygynous nests contained 6–12 (\bar{x} = 9) cells. Somewhat sinuous tunnels, 4.5–7 (\bar{x} = 5.5) mm in diameter, extended below the cell clusters to depths of 7.0–25.0 (\bar{x} = 17.7) cm. Polygynous nests had 1–3 tunnels, but nests built by solitary females had only one tunnel.

The delicate brood cells were constructed of fine sand particles held in a stiff matrix of Dufour's gland secretion. The thinnest parts of the walls of some cells were translucent, and only 0.30 mm thick. The outline of each cell was visible on the surface of the brood comb. Cells (N = 22) were horizontal, of the usual halictine structure (Michener 1974), and 9.0–13.4 (\bar{x} = 11.0) mm in length, and 4.5–5.0 (\bar{x} = 4.8) mm in maximum width. The cell entrances were 1.8–3.7 (\bar{x} = 2.7) mm wide, and they were filled after oviposition with a loose plug of soil that was 1.0–3.5 (\bar{x} = 2.0) mm deep.

Each arched, white egg was laid on a moist, yellow, roughly oval pollen and nectar mass 4.3–4.5 mm long, 3.0–4.3 mm wide, and

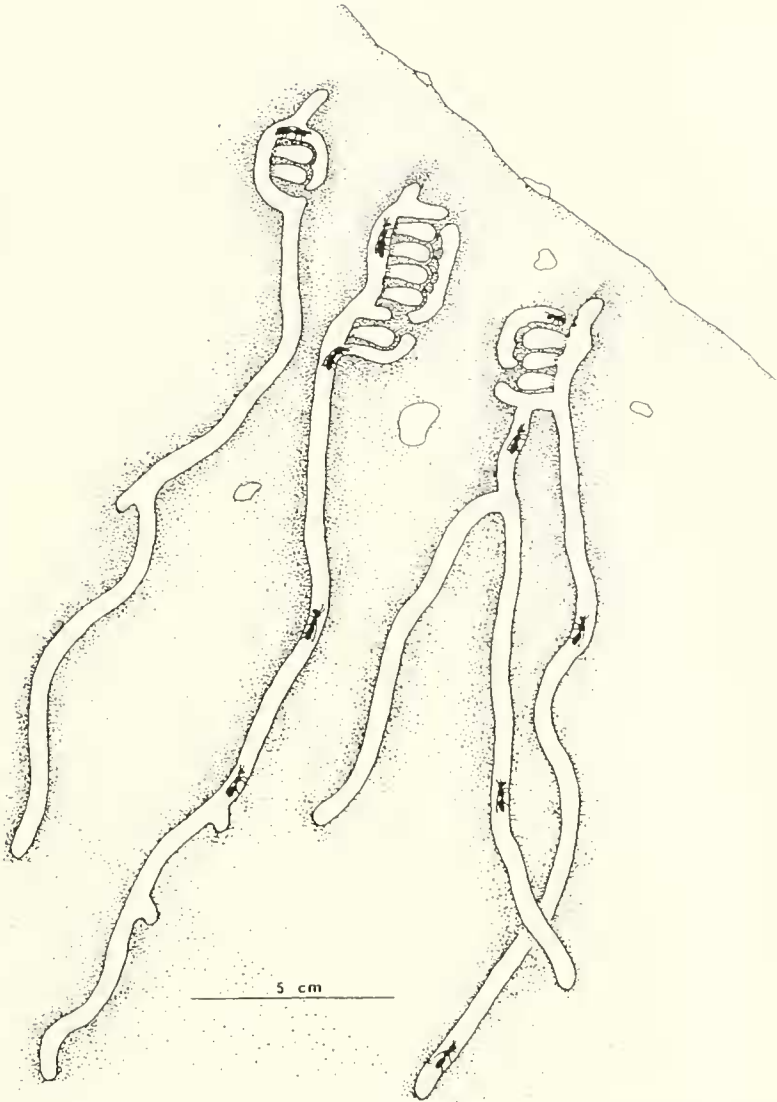


Fig. 1. Three nests of *Evylaeus comagenensis* in the sandy bank. The clusters of cells, each surrounded by an airspace, are in the sun-warmed layer near the surface. The bees will deepen the burrows below the clusters for use as hibernacula.

2.5–3.7 mm high. The provisions were longitudinally grooved on top, and were supported below on a wide pedestal as in *E. linearis* (Knerer 1983), which minimized contact with the cells.

Nests were initiated in late May. During the first week of June, eggs, larvae and pupae were present, with medium-sized to large

larvae and prepupae predominating. By June 10–11 (both years) oviposition had ceased, ovaries were regressing, and the brood included larvae and pupae. I removed these and reared them in plastic tissue-culture wells at 25°C. By June 24, all were prepupae to black pupae, and from June 30 to July 2, adults emerged. Adults were kept in a small,

screened cage outdoors (in Maryland), provided with various cut flowers and sand for nesting. Males patrolled and attempted to mate at flowers, but did not inseminate females (as determined by dissection). All adults disappeared by July 15. The females burrowed into the sand and exhibited a strong photophobic response when they were removed from their burrows in August. Their burrows were initiated beneath objects on the surface of the sand, extended to the bottom of the cage, and each contained up to three females.

Hibernation in nature occurred at the ends of the burrows that extended below the cell clusters. I excavated some nests on October 30, 1987, when soil temperatures were 12°C at the surface, 10°C at 2.5 cm, 8°C at 7.5 cm, 5°C at 15 cm, and 3°C at 20 cm where bees were found. Below that level, the earth was frozen and it was not possible to excavate or locate bees. According to Sakagami et al. (1984) hibernating *Evylaeus* and other halictine bees are capable of supercooling.

The cells of *E. comagenensis* were constructed unusually near the soil surface. Such shallow placement maximized heating during the relatively few sunny days in May and early June (17%, 37%, and 24% of days in 1986, 1987 and 1989). On sunny days, the afternoon soil temperature at 2.5 cm was 10–15° warmer than soil at 15 cm, and 2–5° warmer than soil at 7.5 cm (3 measurements). When the air temperature was 32°, soil at 2.5 cm deep was 40°, and at 7.5 cm deep it was 35°. Packer (1990a, b) found that pebbles or stones just above shallow cell clusters in level soil in Nova Scotia enhance heating.

In 1989, there were fewer nests (3 nests/m²) than in 1987 (9.6/m²). Probably the prolonged heat (many days above 32°) and the June drought of 1988 resulted in high brood mortality. However, the population size of *Andrena alleghaniensis* at this site appeared normal (this species makes cells at 13–23 cm depth, in cooler, moister soil). *Augo-*

chlorella striata (Prov.), another halictine that makes shallow combs, similarly suffered high pupal mortality during an unusually hot, dry summer (Packer et al. 1990b). Because *E. comagenensis* is univoltine, it has no opportunity to rapidly recover population levels. Other species of *Evylaeus* that make shallow brood cell clusters in spring make additional cells at deeper levels for summer broods, thus, they can repopulate more rapidly. Examples are *E. duplex* (Dalla Torre) (Sakagami and Hayashida 1961, 1968, Sakagami et al. 1984), *E. affine* (Smith) (Sakagami et al. 1982) and *E. nigripes* (Knerer and Plateaux-Quénu 1970). A close relative, *Evylaeus nupricola* (Sakagami), is a solitary, univoltine alpine relict species that also makes shallow cell clusters (Sakagami 1988); its distribution may similarly be limited by heat or drought.

In 1987, 82% of nests also included females and larvae of the scutacarid mite, *Imparipes apicola* (Banks) in some of the cells that contained eggs, larvae, and prepupae. In 1989, only 14% of nests included mites. According to Eickwort (1979), these mites feed on the feces of the larvae of various halictid and andrenid bees. Other associates included unidentified nematodes and fungi on feces in cells that contained healthy prepupae, and a conopid larva (probably *Thecophora occidentis* (Wlk.), Knerer and Atwood 1967) in the abdomen of a dead female. Species of *Sphcodes* (Halictidae), *Leucophora* (Anthomyiidae), and *Phrosinella aurifacies* Downes (Sarcophagidae) followed returning foragers, entered nests, or both, but none were found in cells. Larval rhipiphorids and larval Strepsiptera were on adult bees or in their crops, but none were recovered from cells or brood.

SOCIOBIOLOGY

One possible effect of the low population density following the 1988 drought was the lack of polygynous nests. All of the nine nests that I examined in 1989 were occupied by a single female; however, in 1987, 64%

of 12 nests were polygynous. Thus it appears that *E. comagenensis* was only facultatively polygynous. Possibly the solitary foundresses were the only survivors among sisters that would have nested together following a favorable year. Perhaps when competition for suitable nest sites became less, few females joined already occupied nests. In the strictly solitary species, *E. oenotherae* (Stevens), some females attempt to join other nesting females, but they are rejected (Knerer and MacKay 1969). Similarly, solitary *E. duplex* foundresses are aggressive toward strangers, although they later cooperate eusocially with their own daughters (Sakagami and Hayashida 1961).

All females of *E. comagenensis* were inseminated ($N = 56$) and male production was high in my study. Thus this bee resembled a solitary species (see Packer and Knerer 1985). In 1987 and 1989, broods were 38% and 75% male, respectively. Plateaux-Quénu (1967, Fig. 1) indicates a 50% sex ratio for this species. Fluctuating sex ratios occur also in *E. duplex* (Sakagami and Hayashida 1961).

There was neither clear division of labor nor size difference among females that shared the polygynous nests. I measured head width, ovarian and Dufour's gland enlargement, front wing nicks, and degree to which the mandibles were worn down by

Table 1. Contents of polygynous nests of *E. comagenensis* in 1987. Head width units (bee size): 1 mm = 6.4 units. The ovarian development of each female is indicated thus: A, with 2 or more eggs ready to lay; B, with large ovaries, 1 egg ready to lay; C, with moderately developed or regressing oocytes; D, with slight enlargement of oocytes; E, with no oocyte enlargement. Nicks in forewings counted (if x, wings badly damaged). Mandibular wear ranges from 1, with unworn, sharp mandibles, to 5, mandibles worn to stubs, lacking a notch.

Nest	Adults Head Width (in Units), Ovary, Wing Nicks, Mandible Wear	Number of Immatures							Date
		Eggs	Larvae			Prepupae	Pupae		
			Small	Medium	Large		Male	Female	
1. 6 bees	13.5, C, 0, 3 13.5, B, 4, 5 13.0, C, 9, 3 13.0, B, 1, 2 12.5, D, 2, 3 12.0, B, 2, 4	1		2	3				June 1
2. 5 bees	14.0, C, 2, 4 13.5, A, 6, 5 13.0, C, 1, 2 13.0, C, 2, 5 13.0, D, 1, 2	1		3	4	3			June 4
3. 3 bees	14.0, A, 1, 5 12.0, D, 6, 3 11.0, D, 1, 5			2	2	1	1		June 4
4. 4 bees	14.0, D, 8, 3 13.0, C, X, 5 12.5, C, 2, 5 12.0, D, X, 4		1	2	5	2			June 7
5. 2 bees	14.0, D, 0, 3 13.5, E, 4, 5 (forager)		2	1	1	5	1	1	June 7
6. 3 bees	13.0, C, X, 5 12.5, E, 5, 5 12.0, E, 3, 2			2		3	3		June 10

digging, in order to detect possible castes (Table 1). Bees that had eggs ready to lay ($N = 12$) had mean head widths only 1.02% larger than bees ($N = 9$) with undeveloped ovaries (bees with partly enlarged oocytes were omitted from these comparisons). In 1987, 29% of all females had large oocytes, but in 1989, 56% of females, all of which were alone in nests, had eggs ready to lay. There was no consistent difference in wear between egg layers and non-egg layers in polygynous nests. The wings of the egg layers had 1–9 ($\bar{x} = 3.3$) nicks, indicating probable foraging activity, and their mandibular wear was 2–5 ($\bar{x} = 4.0$). Non-egg layers had 1–8 ($\bar{x} = 3.8$) wing nicks and mandibular wear of 3–5 ($\bar{x} = 3.8$).

Nests that were occupied by solitary females in 1989 had 1–7 ($\bar{x} = 3.6$) cells; in 1987, solitary females made 2–5 ($\bar{x} = 3.3$) cells. Polygynous nests with 3 females (1 egg layer) had 3–6 ($\bar{x} = 4.5$) cells; a nest with 4 females (1 egg layer) had 10 cells; a nest with 5 females (1 egg layer) had 12 cells; and a nest with 6 females (4 egg layers) had 6 cells. It was difficult to estimate productivity because of the probability that most or all of the females in polygynous nests may become capable of oviposition at some time. Oophagy and drifting of females to adjacent nests may also occur. It thus appears that polygynous nests more closely approach the democratic quasisocial arrangement than the semisocial pattern of behavior, in which queens and workers are well differentiated. Packer et al. (1990a) found 1–4 females per nest in Nova Scotia, where there appeared to be some division of labor in polygynous nests.

Now that many researchers worldwide have begun to investigate the intricacies and complexities of halictine sociobiology, previously unknown and sometimes unique patterns are revealed, and previously known ones are reclassified. *Evyllaenus comagenensis* has pioneered social and architectural systems that are particularly well suited to the efficient exploitation of resources during

the cool, rainy, and short boreal flowering season.

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